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THE BEARING OF TERATOLOGICAL DEVELOPMENT IN NICOTIANA ON THEORIES OF HEREDITY[1]

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It is desirable, though difficult, to atack genetic problems by both pedigree-culture and cytological methods. It is desirable because the problems are viewed from different standpoints; it is difficult because few forms are especially favorable for either kind of work. The present paper is a preliminary report upon certain characters in a species fairly desirable from each point of attack.

Among plants teratological phenomena are common, especially those known as fasciations, Masters[2] citing, in 1869, 120 genera in which they were not infrequent.

The term fasciation is a broad one and includes, from a genetic standpoint, some very different phenomena. At least two distinct kinds of variation are now emphasized in genetic work, somatic and germinal, although often it is impossible to distinguish between them except by experimental cultures. Fasciation is a phenomenon of variation in which both types occur, though the evidence on this point is not all that could be desired. All observers agree that the fasciated character is constant and heritable in such races as *Celosia cristata*[3] (cockscomb), *Pisum sativum umbellatum*,[4] *Sedum reflexum cristata*,[5] some races of *Zea mays* and *Nicotiana*

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[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

[2] Masters, M. T., ''Vegetable Teratology,'' pp. 9–21, London, 1869.

[3] De Vries, H., ''The Mutation Theory,'' **2**: 68, 516–519, 1910; also Lynch, Irwin, ''Evolution of Plants,'' *Journ. Roy. Hort. Soc.*, **25**: 17–31, 1900.

[4] De Vries, H., *ibid.*, p. 513, 1910. See also Lynch, I., *ibid.*

[5] Masters, M. T., *ibid.*, pp. 18–19, 1869.

[6] East, E. M., and H. K. Hayes, ''Inheritance in Maize,'' *Conn. Agr.*

tabacum fasciata. On the other hand, many examples of fasciation are slight or severe somatic modifications, no more permanent than a swollen limb due to a bruise in our own bodies, or a bone spavin in a horse's foot, though the tissue proliferation may remain as a lasting scar. Examples of this form may be found in *Œnothera*,[7] *Nasturtium*,[8] *Picris hieracioides* and *Raphanus raphanistrum*.[9] Such modifications are imperfectly understood, but may be brought about directly or indirectly by external agencies such as bruises, culture methods and insect injuries to the initial meristem.

Aside from the work of Mendel[10] and De Vries,[11] the phenomena of fasciation have not been dealt with in the light of modern genetics. Mendel's investigations were made on a fasciated strain of pea (*Pisum sativum umbellatum*). When crossed with a non-fasciated strain the teratological character was recessive and segregated in F_2 in a simple 3:1 ratio. This result was essentially confirmed by Lock and Bateson, although environmental conditions were found by them to affect the character more than is usual in such phenomena.

De Vries failed to distinguish between fasciations strictly heritable and those non-heritable. The only con-

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Exp. Sta. Bull., No. 167, and Contrib. from Lab. of Genetics, Bussey Inst. of Harvard Univ., No. 9, p. 133, Pl. XXII (*a*) and (*b*), 1911; also Emerson, R. A., personal communication, 1911.

[7] Knox, A. A., "Induction, Development and Heritability of Fasciations," Carnegie Inst. of Wash. Pub. **98**: 1–21, Pls. I–V, 1908.

[8] Knox, A. A., *ibid.*, p. 14.

[9] Molliard, M., "Cas de virescence et de fasciation d'origine parasitaire," *Rev. Gén. de Botanique,* **12**: 323–327, 1900; also Godron, A., "Mélanges de teratologie végétale," *Mem. Soc. d. Sc. Nat. d. Cherbourg,* **16**: 81–127, pp. 96–97, 1871–1872.

[10] Mendel, G. J., "Versuche über Pflanzen-Hybriden," *Verh. Naturf. Ver. in Brünn,* **10** Abh., p. I. See Bateson, W., "Mendel's Principles of Heredity," pp. 322, 328, 330, Cambridge Univ. Press, 1909.

[11] De Vries H., *ibid.*, III, "The Inconstancy of Fasciated Races," pp. 488–526, 1910; "Monstruosités héréditaires offertes en échange aux Jardins Botaniques," *Bot. Jaarboek,* **9**: 62–93, 1897; "Over de erfelykheid der fasciatiën. Avec un résumé en langue française," *Bot. Jaarboek Dodonaea,* **6**: 72, 1894; "Sur la culture des monstruosités," *Comptes Rendus,* **128**: 125, 1899; "Sur la culture des fasciations des espèces annuelles et biannuelles," *Rev. Gén. de Bot.,* **2**: 136, 1899.

stant fasciated race[12] with which he worked is the cockscomb and his experimental researches on this plant led him to conclude that "complete atavists," or normal plants carrying the fasciated character in a latent state, are very rare, and even under repeated selection are to be obtained in very small numbers. Further, the normal plants thus obtained do not breed true, but revert very soon to the abnormal condition. While investigations have not been made showing definitely that many of De Vries's fasciations were not heritable, but were simply somatic modifications, enough evidence is at hand from numerous sources to justify at least the expression of a strong doubt of their heritable character. According to the observations of Knox, fasciated stems in Œnotheras are not germinal in origin, but traceable directly, in most cases, to insect injuries. Observations by Molliard on *Raphanus* and *Picris* support this conclusion, while Godron was unable to secure fasciated individuals from the seeds of a *Picris* plant thus affected. The fact that fasciation appears in every generation of *Œnothera* plants in varying percentages, in certain cultures, especially those of a biennial nature, is best explainable on a re-infection basis. Spiral torsion races such as *Dipsacus sylvestris torsus* in De Vries's cultures behaved, from a genetic standpoint, in the same manner as his fasciated races. Races of *Dipsacus* species are rich in torsions in Holland and Denmark, but, according to Johannsen,[13] the seeds of torsus strains when grown in England produced normal progeny. This would indicate an environmental rather than a germinal basis as a causal factor.

In all of De Vries's experimental cultures of fasciated races (with the exception of *Celosia*) only a certain per cent. (averaging in most races 50 per cent. or less) of the individuals in each generation possessed the abnormality, and he was never able to breed a constant and genetically pure race. Even though he had been able to do this, doubt could still be cast upon the belief that he was dealing with a strictly heritable character, because the only method that seems to preclude doubt is crossing with the normal and securing the F_2 ratio. This method would eliminate the suspicion that minute bacterial or even ultra-microscopic organisms were acting as causal agents.

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[12] Possibly *Geranium molle fasciatum* may be an exception in which more than one unit factor is responsible for the anomaly. Otherwise it should have bred true at least by the sixth generation if the seed sown each year was from carefully guarded plants.

[13] Johannsen, W., public lecture IV, Boston, 1911.

Emerson and East in their maize studies have obtained races breeding constant for fasciated ears. I have myself examined such a race in Emerson's cultures. Hus, on the other hand, with the same sort of an abnormality in the same plant species, *Zea mays,* secured results similar to those of De Vries.[14] Is the difference in results due to methods or to the nature of the plant abnormality itself? I shall consider the results of De Vries and others holding similar opinions in greater detail in a later paper, as such results entail an extended review.

THE PROBLEM AND THE MATERIAL

The problem to be discussed briefly in this paper is the relation of the cytological phenomena in the reduction divisions to certain segregating Mendelian characters, and the nature of these characters in development and inheritance.

The material upon which the study is largely based is a fasciated variety of *Nicotiana tabacum.* Although fasciations are very common in many genera and not infrequent in others, they have never been recorded (so far as I can determine) in *Nicotiana.* The present race was obtained from the selfed seed of a mutant found growing in a field of Cuban tobacco in the district of Partidos, near the town of Alquiza, Cuba, in 1907. I am indebted to Dr. E. M. East and to Mr. J. S. Dewey[15] for data on this race, prior to the summer of 1910. The sport is characterized by a flattened, fasciated condition of the stem and floral structures, and a consequent increase in the number of leaves. The original mutant is described by Dewey as possessing 152 leaves on the main stalk, flowers abnormal, stem fasciated. When the abnormal plants were studied in more detail, many smaller teratological features were found, and these were especially plentiful in connection with the floral structures. The pistil frequently was incapable of functioning, because of various forms of tissue proliferation in the region of the stigma. The style was often shortened, coiled or fused near its base with an anther (staminody of the pistil). The ovary locules were very much increased in number, ranging from two (extremely rare) to as high

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[14] Hus, H., and Murdock, A. W., "Inheritance of Fasciation in *Zea mays,*" *Plant World,* **14**: 88–96, 1911.

[15] Mr. J. S. Dewey is superintendent of the United States tobacco plantation belonging to the same company that controls the Cuban plantation near Alquiza.

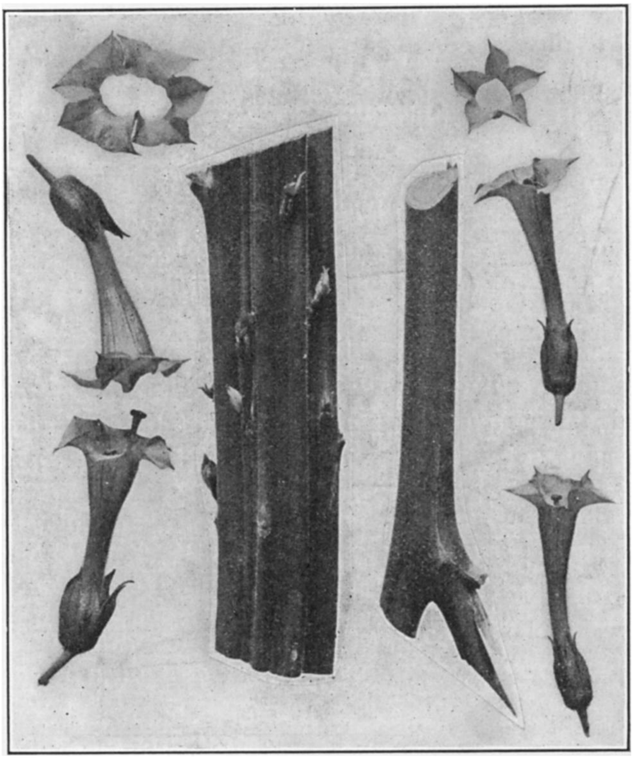

FIG. 1. Stems and flowers from the abnormal and normal strains of N. tabacum.

as twenty. Very often two or even three distinct pistils were formed in the same flower, all of which in some cases could function. The stamens were affected in both filament and anther. The filaments were often coiled, twisted, shortened or fused to the corolla. In rare cases, they were petaliferous. The anther deformities consisted of split anthers, anthers with small pistils growing from them—two or three to an anther being present in one case (pistillody of the anthers). The number of pollen sacs varied from the normal four to six.

The corolla and calyx were often split, and the lobes of the calyx and not uncommonly of the corolla, were irregular in size and shape. Occasionally the calyx and corolla merged into each other by a spiral twist. Two flowers sometimes were enclosed by the same calyx. Once or twice flowers have been found consisting of only a corolla and a few stamens, growing on the side of the normal corolla and partly fused with it. The corollas never show a doubling phenomenon to accommodate the increase in petal number but the circumference of the flower is extended, and very often these flowers are as regular and symmetrical as those of the normal. Two cases of leaves fused at the base have been found and the phyllotaxy is altered and irregular. The fasciated plants when young are practically indistinguishable from the normal. The anatomical features have not been investigated sufficiently for a report upon them at this time, and it is possible that differences between the normal and abnormal seedlings will be found when this part of the study is completed.

Five generations of the abnormal strain have been grown, amounting in all to over a thousand plants, and each individual plant has possessed the unmistakable characters of the original mutant. The monstrous character is, however, a variable one, since the stems may be extremely flattened throughout the greater part of their length or only flattened and fasciated toward their apical ends. Other characters, as already implied, fluctuate between extremes, depending in part on environment

A COMPARISON OF CERTAIN CHARACTERS OF THE F_1 AND F_2 GENERATION OF

303–1–12 is a type of extreme abnormalness. 301–1–2 represents the extreme *tabacum*. (304 × 402)–1–10 = normal F_2 segregate. (304 × 402)–1–12 = abnormal heterozygous F_2 segregate similar to the F_1 (304 × 402)–30.

		Stem	No. of Leaves	Height, In.	Flower	1	2	3	4	5	6	7	8
♀ P	303–1–12	V. abn.	69	76	Sepals . .	7	6	6	7	6	8	9	7
					Petals . .	12	9	6	10	11	12	11	13
					Stamens	12	12	7	12	8	13	11	12
					Ovary locules.	3–3–3	3–3	4	3–3–2	4–3	4–4	3–3	6–3
	301–1–2	N.(?)	33	68	Sepals . .	6	6	7	6	7	6	6	6
					Petals . .	7	6	7	7	8	8	7	7
					Stamens	7	6	6	7	7	7	7	7
					Ovary locules.	3	3	3	3	3	3	3	4
♂ P	402	N.	24	72	Normal as in (304 × 402)–1–10								
F_1	(304 × 402) –30	N.(?)	26	87	Sepals . .	6	6	7	6	6	6	5	6
					Petals . .	7	6	7	6	5	6	5	7
					Stamens	7	6	7	6	6	6	5	7
					Ovary locules.	3	3	3	2	2	3	2	2
F_2	(304 × 402) –1–10	N.	24	75	Sepals . .	5	5	5	5	5	5	5	5
					Petals . .	5	5	5	5	5	5	5	5
					Stamens	5	5	5	5	5	5	5	5
					Ovary locules.	2	2	2	2	2	2	2	2
	(304 × 402) –1–12	V. abn.	80	75	Sepals . .	10	12	6	8	10	7	8	9
					Petals . .	12	20	8	12	15	8	21	12
					Stamens	16	15	7	8	12	7	18	12
					Ovary locules.	6–10	6–3–4	5	3–3	3–4	4	6–4–2–2	4–3
	(304 × 402) –1–34	S. abn.	63	75	Sepals . .	8	7	7	7	7	6	6	6
					Petals . .	8	8	7	7	7	7	7	8
					Stamens	7	8	7	7	8	7	7	8
					Ovary locules.	3	3	3	3	4	3	3	3
	(304 × 402) –1–6	N.(?)	32	75	Sepals . .	5	6	6	6	7	5	6	6
					Petals . .	5	6	6	6	7	5	7	6
					Stamens	5	6	6	6	7	5	7	6
					Ovary locules.	2	3	2	3	3	3	3	3

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[16] Double flower.

ABNORMAL × NORMAL *Nicotiana* (304×402) WITH THOSE OF THE PARENT STRAINS

variation of the abnormal characters toward the normal. 402 is the normal *N.* F_2 segregate. (304 × 402)–1–34 = heterozygous F_2 segregate. (304 × 402)–1–6 =

9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
8	7	7	6	7	7	6	6	6	8	8	7	6	6	7	7	7	
11	12	11	10	8	8	7	9	9	16	8	10	7	7	11	7	11	
11	14	11	12	9	8	7	11	8	17	9	12	7	6	11	7	11	
3–3	4–6–4	5–3	3–4	3–3	5	4	3–2	4–4	8–5	5	2–4	3	3	3–1	3	3–3	
8	7	6	7	8	7	6	6	6	6	6	7	7	6	6	6	6	8[16]
8	7	8	7	8	8	9	8	7	7	7	7	8	7	8	8	5	7
10	7	6	7	7	7	8	9	7	6	6	7	7	6	8	7	5	7
4–2	4	3	3	4	3	3	2–3	4	4	3	3	3	3	4	3	3	3
Normal as in (304×402)–1–10																	
5	7	7	6	6	6	6	6	6	7	6	5	5	5	5	7	5	
5	7	6	6	7	6	6	7	6	7	6	6	6	5	6	7	7	
5	7	6	6	6	6	6	7	6	7	6	6	6	5	5	7	7	
3	2	3	2	3	3	3	3	3	3	3	3	3	2	3	3	2	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
7	8	8	12	7	10	6	7	8	8	7	7	7	7	8	7	8	
10	9	18	24	12	15	8	8	10	15	12	15	8	8	9	12	8	
7	9	16	24	8	18	7	7	6	15	8	10	7	8	8	10	8	
3	4–3	4–4–4–3	7–6–4–4	4	4–4–2	3	4	3	5–3	3–2	4–3	4	5	4	3–4	3–2	
8	7	8	9	8	7	8	7	8	7	12	9	8	8	8	12	11	
8	7	7	11	8	7	8	7	9	7	16	12	11	14	8	12	18	
7	7	8	10	7	7	7	7	9	7	16	12	11	14	7	12	15	
4	3	4	4–4	3	3	3	3	4	4	4–6–4	4–3	4–4	4–4	2	2–2	4–5–4	
5	5	5	5	6	6	6	6	6	5	5	5	5	6	6	5	6	
6	6	5	6	7	7	6	6	6	6	7	6	7	7	7	5	7	
6	6	5	6	6	7	6	6	6	6	6	5	7	6	6	5	7	
2	3	2	3	3	3	4	3	3	3	3	3	3	3	3	3	3	

and in part on the *innate* nature of the character itself. One may confuse this fluctuation to the arc made by a swinging pendulum. The arc through which the pendulum can swing is limited, but within those limits the arc may be medium, large or small, depending on the agencies that set the pendulum in motion. Agencies very different in nature may produce the same result. The pendulum is the material body which makes the arc recognizable as an entity, and in this simile may be compared to the gene for fasciation. When the pendulum is motionless, there is no arc, and there would be no fasciation if the gene remained potential.

A more definite idea of the characters of the plant and their variability may be secured by consulting the table on page 212. It should be stated that plants have been grown under many environments and with many variations in culture. But so far as our present interest goes, no very great changes have resulted. The race has always been clearly distinguishable in the adult state from the normal, whether grown under cramped greenhouse conditions, or out-of-doors; whether surrounded by a Cuban or a New England environment. No especial care, such as De Vries prescribes, regarding culture and transplantation has been given, and yet the anomaly has always bred absolutely true and no "atavists" have appeared.

The normal Cuban variety from which the fasciated strain arose is characterized by a normal round stem, regular phyllotaxy, flowers with five petals, sepals, stamens and a two-loculed ovary. The number of commercial leaves varies between 20 and 25, all leaf counts in the present investigation, being made by the commercial method.[17] Fertility is practically 100 per cent. Occasionally among hundreds of flowers examined a flower is found with an extra sepal or petal, otherwise abnormalities are unknown in our cultures of the normal variety.

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[17] All leaves were recorded up to the first leafless branch ("bald sucker"), exclusive of the first three basal leaves.

In the cultures at the Bussey Institution of Harvard University the normal Cuban is known as 402: the fasciated strain as 300–309, the range in numbers representing an attempt at selection.

METHODS

Data were collected on each plant and tabulated separately. The characters noted were, extent of fasciation in the stem; number of leaves, petals, sepals, stamens and ovary locules. Twenty-five flowers were taken from each plant and the parts of each flower recorded separately. In all crosses made the flowers were castrated in the bud and bagged. Pollen was taken only from anthers still in the closed bud and 95 per cent. alcohol was liberally used after each operation on hands and instruments. The Webber system of recording the plants by number was used. All seed was sown in sterilized soil and all possible care taken to avoid mixtures.

EXPERIMENTAL WORK

Numerous crosses were made between distinct species and the abnormal race, but all of the progeny were sterile, though the abnormal character was visible in their flowers and in the increased number of leaves which they bore.

Four crosses were made between normal *N. tabacum* varieties and the abnormal, all of which produced fertile F_1 plants. The most interesting of these is a cross of the abnormal with the normal Cuban variety from which it mutated. Three generations of this cross (304 × 402) have been grown. The F_1 generation consisted of 39 plants, the F_2 of 97 and the F_3 of 647, totaling 783 individuals. The F_1 was intermediate in character between the two parents, as the table will show. The F_2 gave the three expected types in the ratio of 1:2:1, the actual numbers being:

	Normal	Heterozygote	Abnormal
Actual	28	52	17
Expected	24	48	24

The F_2 selections gave the results expected in F_3. Counting the total progeny (248) from F_1 and F_2 heterozygotes, the figures are:

	Normal	Heterozygote	Abnormal
Actual	68	124	56
Expected	62	124	62

The F_2 heterozygotes were in appearance duplicates of the F_1 individuals and after a little experience could be easily distinguished from the abnormal homozygotes. Clean segregates were obtained from the heterozygous

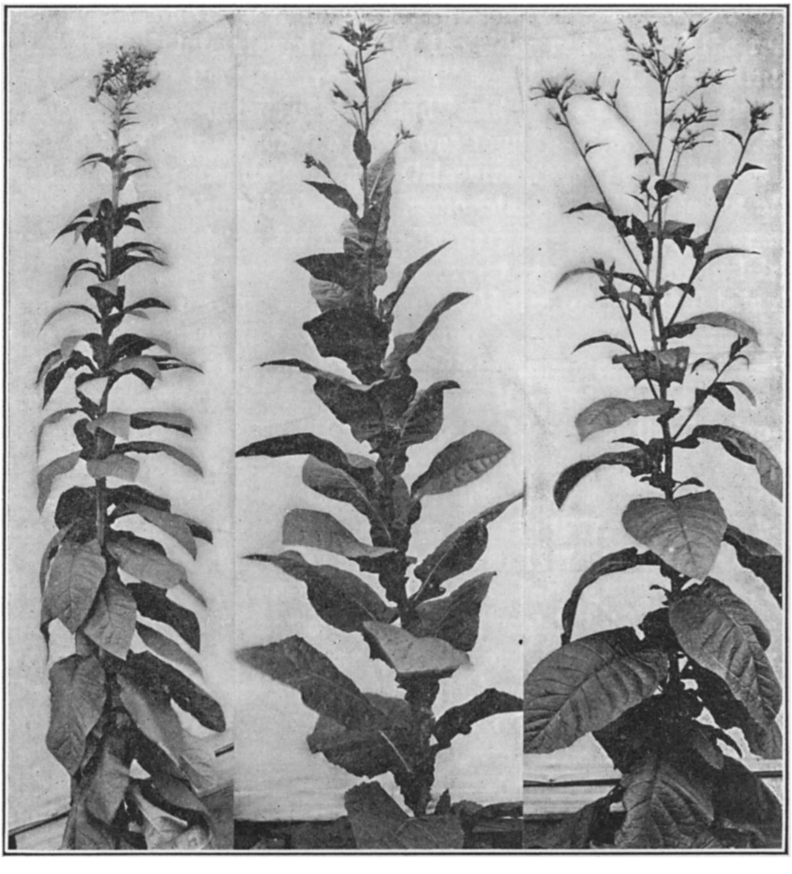

FIG. 2. F_2 segregates from the abnormal × normal (304 × 402) Nicotiana. Abnormal homozygote, heterozygote and normal homozygote. The grandparents in appearance are duplicates of the two homozygotes

plants in both F_2 and F_3 and the homozygous normals and abnormals obtained in this manner bred true in F_3 and F_4. Not being satisfied that only one factor represented the difference between the normal and the abnormal, I thought that it might be possible, through selection, to secure a normal strain from the abnormal, or at least to modify the unit character, as Castle and his students appear to have done with the hooded pattern in rats.

Selection work was started by selecting from the cultures the most abnormal and the least abnormal plants as seed producers. The work was carried through two generations with no prospect of success and there it remains at present. Progeny of the least abnormal plants were as much fasciated and otherwise abnormal as the original parent strain growing beside it. And one could not distinguish the least abnormal from the most abnormal strain except by the label. So far as the work has progressed, this fasciated strain seems no more amenable to selection than the cockscomb with which De Vries worked, and of which he said "at present at least there seems not to be any prospect of obtaining a pure atavistic strain."[18]

From a comparison between the drawing in Gerarde's Herball of 1597[19] and certain woodcuts from old horticultural magazines with the plants as they are to-day, it does not appear that much change has taken place in the cockscomb fasciation since its introduction into Europe in 1570.

The changes in the expression of the comb that gardeners and florists will maintain have taken place as a result of selection can all be accounted for by the influence of the environmental factor.

Lock planted seeds of very slightly fasciated individuals of the F_2 generation of normal × fasciated stem in *Pisum*. The F_3 plants were almost, if not as much fasciated, as the original grandparent strain.[20]

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[18] De Vries, H., "The Mutation Theory," 2: 519, 1910.

[19] Gerarde, John, "Herball or Generall Historie of Plantes," 1st ed., pp. 323–325, Fig. on p. 323, 1597.

[20] Lock, R. H., *loc. cit.*, p. 106.

This fasciated strain of pea (Mummy Pea or *Pisum sativum umbellatum*) would appear to have been a very constant race, at least since 1597, when it was figured in Gerarde's "Herball."[21]

From the results of hybridization and selection, one may draw the conclusion that the fasciated mutant differed from the normal parent strain by only one factor and that it represents a mutation upon the variability of which selection has no modifying effect. The character itself appears to be due to one underlying cause and its variableness is only the external manifestation of the capricious working of that cause.

After completing a satisfactory study of the gross aspects of this character, a cytological investigation was made, with the hope that here might be found a clue to the cause or causes underlying the appearance of the anomaly.

CYTOLOGY

Much trouble in fixing material was caused through the presence of resinous substances in the tissues. Flemming's medium and strong solutions were finally found to be the most successful, although prolonged bleaching of the sections with H_2O_2 was necessary to eliminate the blackening. Care had to be exercised to secure quick penetration, as poor fixation and shrinkage were likely to result after a bath of over 24 hours. The preparations were stained in Heidenhain's iron hæmatoxylin and counterstained with clove oil saturated with erythrosin. This combination usually gave the best results —a deep black chromatin stain against a brilliant red background. Preparations were also stained with the safranin-gentianviolet-orange G combination of Flemming and restained with iron hæmatoxylin. This method gave very sharp outlines, not easily obtainable in some phases, when the ordinary hæmatoxylin method was used. Another combination which was found valuable in cases where the chromosomes were closely crowded together, as in certain metaphases, is safranin, magdala red and azure II. Large quantities of the fresh material of the anthers in various stages of maturity were stained with methyl green and microscopically examined. In most cases one anther of a bud to be fixed was inspected in this manner. This precaution was necessary as a check on the occurrence of artifacts from fixation.

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[21] Compare with photograph in Darbishire, A. D., "Breeding and Mendelian Discovery," p. 22, Fig. 8, 1911.

Briefly, conditions in the normal Cuban variety (402) are as follows. The ordinary maturation processes are those cytologists have so often described for plants, and need no recapitulation here. The spireme in prophase is single and, just preceding diakinesis, breaks up into segments which take the form of twisted and horseshoe-shaped loops. The latter resemble Davis's figures for *O. grandiflora.*[22] Each loop consists of two spireme segments joined at one end, which in the later heterotypic phases separate and go to opposite poles. Each segment is interpreted as a somatic chromosome, and the members of a pair are homologues. The other phases present nothing peculiar. The homotypic chromosomes appear as entities first in very late anaphase of the first division. The reduced chromosome number, as determined by very numerous counts of heterotypic metaphases and anaphases, and homotypic telophases is 24, the $2n$ being 48. The somatic number ($2n$) was determined by adding together the homotypic telophase chromosomes of a tetrad and dividing the entire number by two. Polar views of the metaphase of the first division in sections of 10μ have repeatedly shown the 24 gemini, each geminal chromosome consisting of a diakinetic pair. Variation of chromosome number in these normal (402) anthers is very rarely, if ever, to be found. None was found in the present investigation. Irregular divisions are not common, although occasionally one sees lagging chromosomes. Usually the phases of a single pollen sac are more advanced at one end than at the other and the maturation processes are at a similar stage in the different sacs of the same anther. Cursory examination of reduction phenomena in the ovule confirmed these observations.

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[22] Davis, B. M., "Cytological Studies on *Œnothera.* I. Pollen Development of *Œnothera grandiflora,*" *Ann. Bot.*, **23**: 551–571, Pl. XLI, Figs. 31, 34, 36, 1909.

Many anthers of the abnormal (300–309) when examined cytologically, were entirely normal in all their phases of maturation. Others showed evidences of almost total sterility through premature breaking down of the archesporial tissue, while still others were only partially sterile. Anthers of this strain were mentioned earlier as sometimes having more than four pollen sacs. In such cases the maturation phases were in very different stages in the different sacs. In one sac the archesporium might be in early prophase, while in other compartments there would be almost mature pollen. This extreme variation in maturation was not confined to anthers with an abnormal sac number, but was often true of those normal in this respect. Conditions in the anthers of the abnormal strain are similar as regards the normal cytological phenomena, but various abnormalities are not uncommon. These manifest themselves in such a manner that one can not avoid believing that some subtle agent is at work here, too, distorting the internal as well as the larger so-called external characters. In both reduction divisions in all the strains examined, various abnormal phenomena are to be found which are not due to fixation or other technical operations. Contrasted with the normal (402) the maturation phases in different sacs of the same anther may be far apart. Nearly mature pollen is present in some sacs, while others in the same anther may not have progressed farther than diakinesis. Pollen tetrads are often rare in nearly mature anthers. This is true of at least five per cent. of those examined. Mother-cells may break down during early prophase, diakinesis or any of the later phases. In early prophase, the nuclear membrane may disappear and the whole archesporium disintegrate.

Again, I have found that in some sacs most of the archesporium has broken down, but some few cells seem to have escaped destruction and matured. The metaphase, so far as I have observed, is not so likely to be disturbed. An occasional premature splitting of the chromosomes takes place, increasing the number to be seen in the polar view of the nuclear plate. These are rare, but they have been observed in both the abnormal strain and the abnormal segregates. This feature has been referred to as a premature splitting,[23] but it may be interpreted as an actual increase in number such as Wilson found in *Metapodius*,[24] Stevens in *Diabrotica*[25] and Strasburger in *Wikstroemia*.[26]

In one pollen mother-cell, 51 chromosomes were clearly distinguishable, but disintegration had already commenced. In another case 30 were counted, the mother-cell appearing perfectly normal, although in the anther containing it irregular divisions were taking place. The nuclear metaphases in which such an increase in number can be seen are rare, but so far as I have observed, and I have counted many nuclear plates ideal for such work, they only occur in the abnormal or in the abnormal segregates. The heterotypic anaphases of the abnormal often show the chromosomes lagging or distributed promiscuously over the spindle. In only one case so far have I found irregular conditions in the telophase and this only in the case of one mother-cell. Counting is unsatisfactory in the anaphase of the first division, as the nucleus is small and the chromosomes are many.

Irregular divisions are present in the homotypic, but most of the abnormalities occur during the heterotypic mitosis.

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[23] Preparatory for the homotypic division.

[24] Wilson, E. B., "Studies on Chromosomes. V. The Chromosomes of *Metapodius*, a Contribution to the Hypothesis of the Genetic Continuity of Chromosomes," *Journ. of Exp. Zool.*, **6**: 147–205, 1909, 1 plate and 13 text figures.

[25] Stevens, N. M., "Further Observations on Supernumerary Chromosomes, and Sex Ratios in *Diabrotica soror*," *Biol. Bull.*, **22**: 231–238, figs. 1–13, 1912.

[26] Strasburger, E., "Chromomenzahl," *Flora*, **100**: 1910.

It is impossible to say whether pollen grains capable of functioning ever result from those divisions where the chromosomes are irregularly distributed. The irregularities in reduction do not produce supernumerary pollen grains, such as have been described by Juel and Strasburger for *Hemerocallis,* for in all tetrads mature enough to show the separation of the pollen grains I have always counted four. One might expect an increase in number of pollen grains formed by one mother-cell, judging from the grosser manifestations of this abnormal factor. Functioning pollen is formed in quantity and no trouble at all is found in securing plenty of selfed seed of the abnormal strain.

Reduction phenomena in the ovule of the abnormal have so far been given only a superficial examination and the observations are not complete enough to report. Observations on the ripe capsules of selfed plants would lead one to believe that here, as in the case of the pollen, partial sterility is present, due to the abortive development of the ovules, but the latter is only a supposition, which further cytological study may or may not support.

Cytological examination of the anthers of the three classes of plants obtained from the abnormal × normal (304 × 402) was made. The conditions in the reduction divisions of the normal and homozygous abnormal segregates are identical with those present in the two grandparents. The heterozygote differs from the pure abnormal in degree only, having fewer sterile anthers and other abnormalities. Otherwise what has been said of the pure abnormal (300–309) applies also to the heterozygote.

In connection with this cross, it is interesting to note what bearing the nature of the reduction divisions in the ovule (300–309) might have upon the F_2 ratio. The abnormal class, although within the probable error, is always deficient. This is true also in the fasciated peas with which Mendel[27] worked and in one race of peas having sterile anthers with which Bateson[28] experimented. While the number of plants has not been large in any of these cases, one wonders why it is always the abnormal (pure) class which is deficient. If the reduction phenomena in the ovules of the abnormal *Nicotiana* agree with the conditions present in the anthers, it seems not unreasonable to believe that there may be a relation between the mortality of the gametes carrying the factor for abnormalness and the deficiency in the ratio. Increased mortality of this class of gametes over the normal class would reduce the chances for combinations of the abnormal gametes, and as a consequence the normal and heterozygote combinations would be increased.

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[27] *Loc. cit.*

SUMMARY OF OBSERVATIONS

Concluding, one must bear in mind that the facts so far obtained seem to warrant the belief that some agent is at work on the internal structure as well as on the so-called external, and is of such a nature as to produce abnormalities in cell structure as well as in cell complexes or plant organs. The data, as a whole, raise a question as to the significance of chromosomes in inheritance.

Two strains of *Nicotiana tabacum* have been investigated, one being a sport from the other. The sport has been shown to differ from the normal in the possession of a unit character due to one Mendelian factor. When it is crossed with the normal, there results in F_2 a simple Mendelian ratio of 3:1 as regards normal and abnormal characters. The heterozygote is, with a little practise, distinguishable, making the ratio 1:2:1 with abnormalness partially dominant. The F_3 generation has proved these segregates to breed true. *Absolutely* clean normal segregates appear in F_2 and breed true. The abnormal character has been described in detail, and shown to affect practically all the structural parts of the plant individual, even to the germ cells. Both strains have the same chromosome number, 48 and 24, as a definite mode.

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[28] Bateson, W., and others, Reports to the Evol. Com., II, p. 91, 1905.

CHROMOSOMES IN RELATION TO MENDELIAN FACTORS AND A PHYSICAL BASIS OF INHERITANCE

Suppose we maintain the factor for the abnormal condition to be a particle of one chromosome. Gametes of the abnormal strain all contain the factor for abnormalness, as reciprocal crosses with the normal give the same results. In a cross a pollen grain of the abnormal strain unites with an egg of normal (402) parentage, and an intermediate is produced in F_1. The chromosome containing the factor for abnormalness is partly neutralized by pairing with a normal homologue. Gametes of two kinds are formed in approximately equal numbers in F_1, those containing the factor for abnormalness and those without it. But on a chromosome hypothesis, how are these gametes formed? There are two reduction divisions and 48 chromosomes, 24 of abnormal parentage and 24 of normal. According to current cytological investigation and interpretation, each chromosome separates from its homologue in its entirety during the first reduction division, so that, eventually, two kinds of gametes are formed as regards chromosomes. The factor for abnormalness or fasciation is in one chromosome, and chromosomes are believed to be in homologous pairs—one maternal with one paternal. The chromosomes of a homologous pair separate during the heterotypic anaphase, one going to each pole, it being contrary to current interpretation to believe that both members of a pair may go to the same pole. On this basis, according to the law of chance, approximately half the nuclei at the end of the heterotypic division will contain the chromosome carrying the factor for abnormalness and from half it will be absent.

Experimentally it has been shown that we have been dealing with only one pair of unit characters and that no complications are present. The various crosses have always given uniform results in F_1, even between species, and the fertile cross has given a close 1:2:1 ratio in F_2. Logically, then, one is led to believe that one out of the

24 chromosomes of abnormal parentage, and only one can contain the factor for abnormalness and produce the experimental results. If more than one contained it, the ratio in F_2 would be changed. For example, if it were present in two chromosomes, the ratio (as suggested by Emerson)[29] must be 15:1 or in this particular case where the heterozygote is distinguishable, 7:8:1. We might postulate its presence in all 24 chromosomes and believe, as Cannon[30] did, that parental chromosomes separate as a phalanx in the F_1 reduction division, each group going to one pole and thereby bringing about the formation of pure parental gametes. But the cytological investigations of Sutton, Rosenberg, Strasburger and others have brought to light evidence which precludes such a supposition. The experimental data from genetic researches are also opposed to this hypothesis, if one attempts to show a relation between the reduction division and Mendelian segregation. On a chromosome hypothesis, then, one *must* believe the factor for abnormalness to be present in only one chromosome out of the 48 concerned in the F_1 reduction phenomena, in order to be in agreement with the experimental results. This being the case, how is one to account for the abnormalities which occur during the reduction divisions in the anthers of the F_1 heterozygote? For they affect, not alone one chromosome, but all the nuclear and cell material concerned in the formation of the pollen grains. Can one postulate the influence of one chromosome to be so great, at times, as to bring destruction to its 23 associates of abnormal parentage, its 24 associates of normal parentage, as well as all the other organized contents of the mother-cell? Why, it may well be asked, if this destruction is the result of the activity of one chromosome does not it take place in the case of every anther and of every pollen mother-cell? Why should it affect only two or three

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[29] Emerson, R. A., "Genetic Correlation and Spurious Allelomorphism in Maize," 24th Ann. Rpt. Nebr. Agr. Exp. Sta., pp. 59–90, 1911.

[30] Cannon, W. A., "A Cytological Basis for the Mendelian Laws," *Bull. Torr. Bot. Club*, **29**: 657–661, 1902.

anthers in a flower containing 8 or 10? Not because it is absent from the other anthers, because the pollen from these anthers transmits the character. It is not a question of segregation then, but one of environment.

Evidently the gene is inactive or latent, for we know there is something present which for convenience we call a gene, and yet we can not see any of the visible signs of its presence, such as we see in the affected anthers. On a morphological conception it must be there; physiologically for the time being, so far as we can determine, it is non-existent. The inactivity we may suppose is due to a lack of a properly adjusted environment. This proper adjustment is only true of a few anthers in the F_1 plants. We believe this scarcity to be due to two kinds of latency —inactivity of the gene as in the pure abnormal and inactivity of the gene because of association with the cell materials that trace their lineage back to the sperm of the normal father. But latency is a vague term. In genetics, it is used to describe the period between the disappearance of a character and its reappearance. By pushing this conception to its logical conclusion it is clear that one can practically never prove the origin of a new character. Fasciation, while new to *Nicotiana,* is phylogenetically an old character. The production of purple fruits in *Rosa* would mean, phylogenetically, the reappearance of a latent character, for purple fruits are common to the *Amelanchiers* and to a species of *Pyrus.*[31]

The characters of the whole plant kingdom would be in a state of latency and patency, of inactivity and activity. To determine whether a character were new or not would involve a canvass of that part of the plant kingdom phylogenetically older than the family under investigation. Of course, we speak of segregation in phylogenetical lines, but the term has a different meaning in such cases. My F_2 normal segregates are pure and will breed true for absence of abnormalness, I believe, for any number of generations unless a new mutation occurs. These recurrent mutations, Johannsen says, are rare in his experience, but they are admitted to occur in almost any long-continued pedigree line, and if fasciation should appear as a repeated mutation after 20 generations of plants involving 2,000,000 individuals had been grown, is one to infer that the gene was present all this time, but latent or inactive? Or is this a new gene produced by the same condition that brought about the original fasciation? Logically, if one defends the latency conception, he must believe that the original gene for fasciation was inactive in all these millions of plants, which in our present stage of knowledge is a ridiculous assumption, since the term is used to describe a somatic appearance. Applied to genetic problems in general, hopeless chaos would result. But on the supposition that a portion of a chromosome is responsible for the abnormality, it seems to me necessary to assume the chromosome to be capable of becoming active or latent without cause. For it seems probable that the anthers are all alike from a constitutional standpoint. How else can one account for the normal anthers and the abnormal ones, the normal pollen mother-cells and those affected by the abnormality?

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[31] *Pyrus Niedwetzkyana.*

The conception of latency is not necessary in the case of complete or incomplete dominance in F_1 hybrids, for in such cases there is evidence that a gene from one parent may be partially or completely inhibited in its expression by factors from the other parent, and this is probably what happens when we bring a line of chromosomes and cell materials from the normal (402) plants and associate them (by fertilization) with a line of cell materials from the abnormal (300–309).

While the phenomena of segregation described in the preceding pages may be capable of interpretation on a morphological basis, the gene for fasciation appears to me to lie deeper in sporogenesis than chromosomes. The abnormal character development appears most easily interpreted from a physiological standpoint. In

F_1 there is no break in the continuity of its manifestations between sporophyte and gametophyte, even though reduction and probably segregation have occurred. And should we not expect to see such a break if segregation by chromosomes took place in sporogenesis?

The evidence as a whole I think, warrants one in the suggestion that chromosomes are characters of the zygote and gametophyte, on the same footing in development with other plant characters. It is more difficult to comprehend this conception of these bodies, because they appear as characters in the development of the cell, rather than in the development of the larger unit, the individual organism. They are characters in the sense that they disappear and reappear at a place and time in the life history of the organism which we can predict. They can be transferred from one race of organisms to another provided fertile F_1 hybrids are possible. They are influenced in as definite a manner, by the underlying cause represented by the term factor for abnormalness, as are the zygotic expressions included in the word fasciation.

Concluding, I realize these speculations are largely negative in character, but they are in accord with a steadily growing skepticism among students of genetics as to the importance of chromosomes in inheritance, and their relation to segregating Mendelian characters. The impression has been distinctly gained from a study of this abnormal strain and its crosses with the normal that chromosomes are not the omnipotent creators of destiny, but characters on the same footing with other structures. The same dynamic forces, whatever they are, are changing and modifying these chromosome characters in the same capricious manner as those of a grosser nature. One would be inclined to ascribe these changes to an ultra-microscopic parasitic organism were it not for the experimental evidence in F_2, which precludes such a belief.

My warmest thanks are due Dr. E. M. East for suggestions and criticisms while engaged in this investigation.

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